New Trends in Soil Biology

Proceedings of the VIII. Intl Colloquium of Soil Zoology. Louvain-la-Neuve (Belgium). August 30 - September 2, 1982. Edited by Ph. LEBRUN, H.M. ANDRÉ, A. DE MEDTS, C. GRÉGOIRE-WIBO and G. WAUTHY. Imprimeur DIEU-BRICHART, Ottignies-Louvain-la-Neuve (1983).

ALLEZ-LES-VERS, a simulation model of dynamics and effect on soil of populations of Millsonia anomala *(Oligochaeta - Megascolecidae)*

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Summary :

Population parameters, vertical migrations and soil ingestion of *Millsonia anomala* were simulated. ALLEZ-LES-VERS is a model with discrete variations of state written in SIMSCRIPT II.5. It gives instantaneous descriptions of the system composed of earthworm entities described by 11 attributes (e.g. age, depth) and grouped in sets (e.g. mature adults, inactive worms). These entities are transformed by events (e.g. hatching, death) or processes (e.g. weight growth, vertical movements) arranged in a time-list according to their time of occurrence. Eight subprograms describe the transformations shown by these events or processes.

Calibration of the model was made with the population of a grass savanna observed in 1972. A population observed in 1969, a very dry year, in a shrub savanna was used for the validation. The results were satisfactory despite some imperfections in the migration submodel and calculation of the nutritive value of the soil that will be easily corrected.

Résumé : ALLEZ-LES-VERS, un modèle de simulation de la dynamique et des effets sur le sol des populations de *Millsonia anomala*

Les variations des paramètres démographiques, les migrations verticales et l'ingestion de sol des populations de *Millsonia anomala* ont été simulées. ALLEZ-LES-VERS est un modèle à variations d'état discrètes rédigé en SIMSCRIPT II.5. Il donne des descriptions instantanées du système composé d'entités Vers de terre décrites par 11 attributs (tels que l'âge, la profondeur) et regroupées en ensembles (tels que les reproducteurs ou les vers inactifs). Ces entités sont transformées au gré d'événements (tels les éclosions ou la mort) et de processus (croissance pondérale, mouvements verticaux) rangés dans un échéancier en fonction de leur temps d'occurrence.

Huit sous-programmes décrivent les transformations entraînées par ces événements et processus.

La calibration du modèle a été réalisée avec une population de savane herbeuse observée en 1972. Une autre population observée en 1969, une année très sèche, dans une savane arbustive, a été utilisée pour la validation. Les résultats sont satisfaisants malgré quelques imperfections dans le sous-modèle de migration et le calcul de la valeur nutritive du sol qui seront aisément corrigées.

Key words : earthworms, simulation model, population dynamics.

I. Introduction

The outlines of the functioning of *Millsonia anomala* populations have been delineated in several papers by one of us (LAVELLE, 1971, 1975, 1978). These studies have mainly focused on demographic characters, effects on the soil and its seasonal changes influenced by main environmental factors. This research has been synthetized in a first version of the present model. The former was composed of four subunits (LAVELLE & MEYER, 1977).

The environmental sub-model, based on the results of a multivariate analysis, determined the soil conditions at each time unit. Individual growth was calculated with a set of equations derived from multiple regressions. Most of the mean annual values of population parameters were correctly simulated by this model; nevertheless, seasonal variations were quite badly simulated. In particular, the use of equations derived from multiple regressions made it difficult to generalize this model to other populations if not to other species.

The growth submodel is the only part of this model that has been kept in the new model ALLEZ-LES-VERS. This and other submodels have been built with sets of empirical laws drawn from the data accumulated over four years of field observation in five different savanna facies and of laboratory cultures.

II. Structure of the model

Millsonia anomala, of the ecological category mesohumic endoges (LAVELLE, 1983), generally lives in the upper ten centimeters of the soil profile and is geophagous. The localization in depth and degree of activity of each worm, as well as the occurrence of the different stages of its life cycle, depend essentially on soil moisture, but also on soil temperature and nutritive value, as well as on the population density. Other factors have not been taken into account, whether they are considered of little importance or already described by any of the precedent factors. They are predation, d~~e~~iseases, interspecific competition, heterogeneity of the environment at the scale of a « homogeneous » facies and seasonal variation of the quantity and composition of organic matter.

Hydric and thermic soil profiles are simulated daily by a special model designed by CLEMENT (1980) and taken into account in the other submodels : « activation-inactivation » that determines whether a worm is active or quiescent, « growth » that calculates the daily changes in individual weights, « mortality », « migration » that simulates the vertical movements of worms in the soil and « reproduction » that simulates cocoon production.

The program gives, each ten days, detailed pictures of the population as well as of the values of the main parameters of its functionning : density, biomass, structure, tissular production and soil ingestion.

1. The simulation program

The program is written in SIMSCRIPT II.5 language (KIVIAT *et al.*, 1973; MEYER & PAMPAGNIN, 1979; MEYER, 1980). The model belongs to the category with discrete variations of states and is based on instantaneous descriptions of the natural system in terms of entities, attributes and sets. Each worm is an individualized entity represented in the computer memory by a series of consecutive *words* corresponding to the different attributes taken into account (Fig. 1).

As simulation develops, the value of each attribute may be modified and new entities created to represent individuals that were just born, or destroyed, when they die. It is possible to group some entities in special conceptual sets (e.g. reproductive worms) or delete entities. The state of the simulated system is represented at any time by the values of each attribute of each memorized entity and the grouping of these entities in any special set. This state varies along with the *events* and processes taken into account. From a programming point of view, they are particular entities grouped in a special set called *event-list*; they are classified according to the value of the one attribute that represents their time of occurrence. Another attribute characterizes the kind of event or the nature of the process they represent.

The event-list is used by the SIMSCRIPT II.5 system to realize the dynamical simulation of the model. The successive entities it contains are processed by order of increasing time of occurrence. As an example, in the case of the event-list of Fig. 2, the simulation clock will be first fixed at 10 and an event or process of the A type be executed. As far as informatic is concerned, this involves a subprogram that describes the consequences of this event or process for the state of the simulated system; the attributes of the « calling » entity can be given as arguments to the « called » subprogram.

When all the modifications of state have been realized, the simulation clock is fixed at time 11.2 and an event or process of the B type is executed *i.e.* all the changes of state that implicate the associated subprogram are executed. The clock will be then fixed at 11.7, time when a new event or process of the B type will be executed.

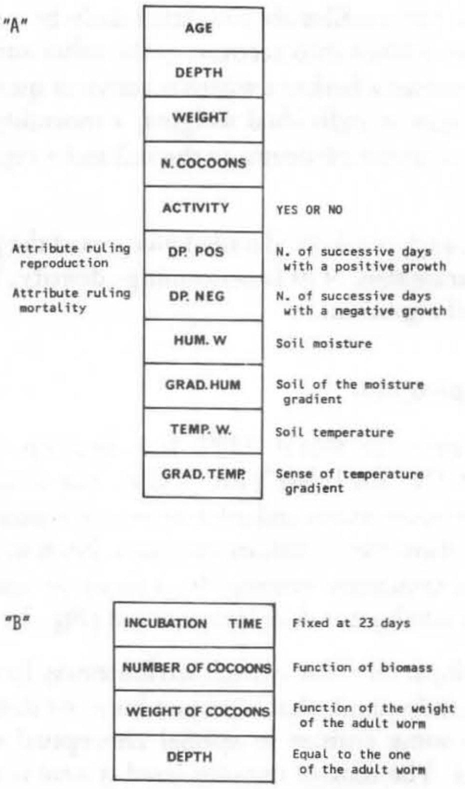
"A"
AGE
DEPTH
WEIGHT
N. COCOONS
ACTIVITY
YES OR NO
Attribute ruling reproduction
DP. POS
N. of successive days with a positive growth
Attribute ruling mortality
DP. NEG
N. of successive days with a negative growth
HUM. W
Soil moisture
GRAD. HUM
Soil of the moisture gradient
TEMP. W.
Soil temperature
GRAD. TEMP.
Sense of temperature gradient
"B"
INCUBATION TIME
Fixed at 23 days
NUMBER OF COCOONS
Function of biomass
WEIGHT OF COCOONS
Function of the weight of the adult worm
DEPTH
Equal to the one of the adult worm

Figure 1 Schematic representation of entities « earthworm » (A) and « cocoons » (B) with the attributes wich characterize them.

At any time, entities can be introduced or taken off the event-list. The execution of the event or process B at time 11.2 may lead to the inclusion of a new entity in the event-list : if its time of occurrence is 18, it will be arranged between the entities with respective times of occurrence 11.7 and 25. In the same way, the performance of the event B at time 11.7 may lead to the suppression of this new entity, or some other one.

In the logic of SIMSCRIPT II.5, an event develops instantaneously, at the time indicated by the « calling » entity in the event-list. A process, on the other hand, has a certain duration : it is « activated » when the corresponding subprogram is « called », it ceases when the designed period of time is over and it may be « interrupted » during a certain period of time which is not deduced from the designed duration.

ALLEZ-LES-VERS involves two kinds of processes : one is *daily cycles*, the other one *incubations* whose duration is predetermined but that may be interrupted. It also involves a series of events, e.g. *hatchings*, that end each incubation process. The simulation consists in carrying out daily the changes of state described in the « daily cycle » process : the attributes of each worm and its possible belonging to the repro-

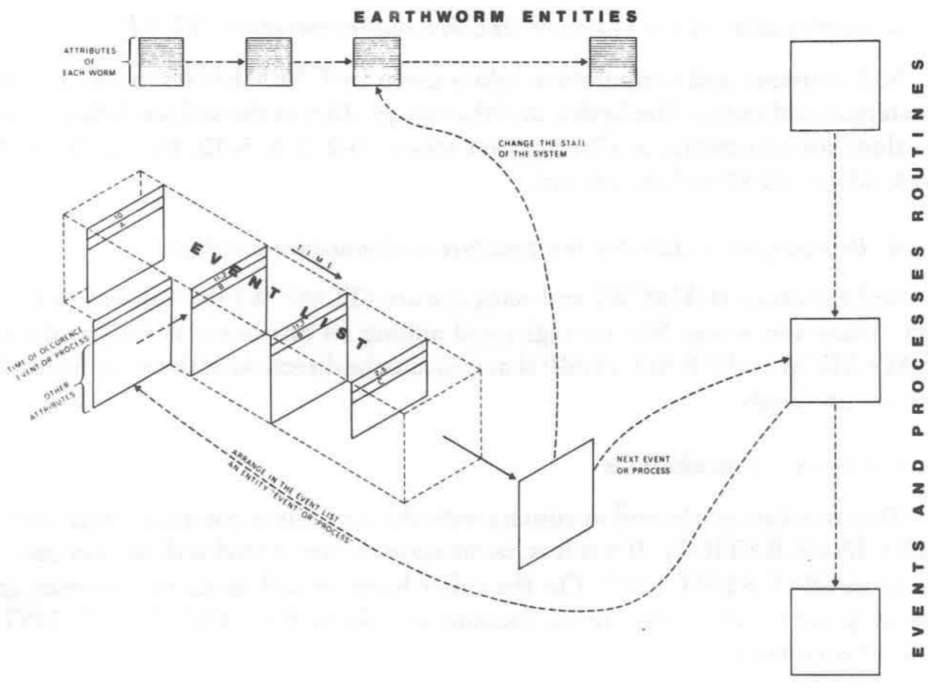
EARTHWORM ENTITIES
ATTRIBUTES OF EACH WORM
CHANGE THE STATE OF THE SYSTEM
10
A
EVENT LIST
TIME
11.2
B
11.2
B
2.5
C
TIME OF OCCURENCE EVENT OR PROCESS
OTHER ATTRIBUTES
ARRANGE IN THE EVENT LIST AN ENTITY "EVENT" OR "PROCESS"
NEXT EVENT OR PROCESS
EVENTS AND PROCESSES ROUTINES

Figure 2 Functioning scheme of the SIMSCRIPT II. 5 system.

ductive set are actualized. Some individuals may die and cocoons be laid which will engage incubation processes that might in their turn be interrupted or reactivated.

The program includes a *preamble*, a *main program* and a series of subprograms. In the preamble, the entities, attributes, sets, events and processes of the model are described. The nature of the different variables and the tables necessary for calculations are specified. The main program is used to initialize the simulated system. It creates the different earthworm entities that compose the population at the beginning of the simulation and arranges in the event-list the entities that represent events or processes that had been engaged before. At last, the subprograms describe the changes of state that will involve the different events and processes that rule the dynamics of the model.

2. Description of the submodels

The daily cycle process involves all the calculations that are repeated each day : bring up to date moisture and temperature conditions, control incubations and activate the five submodels that rule the evolution of the different attributes of each earthworm entity.

a. Daily values of soil moisture (HUM) and temperature (TEMP)

Soil moisture and temperature values given by CLEMENT's model are read on an external card index. The hydric and thermic profiles of the soil are defined each day by values corresponding to 10 successive strata : 0-2, 2-5, 5-10, 10-15, 15-25, 25-35, 35-45, 45-60, 60-80 and 80-140 cm.

b. Bringing up to date the temperature and moisture attributes

Soil moisture (HUM.W) and temperature (TEMP.W) that prevail in the right place where the worm lies are registered among its attributes as well as the values GRAD. HUM and GRAD.TEMP that indicate the direction of the moisture and temperature gradients.

c. Control of incubations

The moisture of the soil in contact with the cocoons is compared with the values SEUIL INCUBATION. If it is less, incubation is interrupted and the cocoons classified in the INT.RUPT.LIST. On the other hand, if soil moisture becomes greater than the predetermined threshold, cocoons are taken off the INT. RUPT. LIST. and incubation restarts.

d. « Activation-inactivation » submodel

When soil moisture drops below 8 % (a value comprised between pF3 and PF4.2), earthworms become quiescent. They are « inactivated » with a probability that depends on HUM.W (p = 1 if HUM.W = 6; p = 0.5 if HUM.W = 8; p = 0 if HUM.W = 12). If HUM.W rises again up to 8 %, the worm is « activated ».

e. Weight growth submodel

The daily rate of weight growth is calculated in three stages. The amount of ingested soil is first calculated from the weight of the worm, soil moisture and temperature, using a set of empirical laws (LAVELLE & MEYER, 1977). The total energetical value of this soil is then determined according to the depth. Finally, laboratory curve sets are used to calculate the daily growth rate from the energy input for a worm of a given initial weight. Soil saturation ($pF < 2$) or an excessive density ($>22.5/m^2$) may have depressing effects on growth.

In the model, the age of the worm is first increased by one day, then its soil ingestion is calculated. If the population density is greater than $22.5/m^2$, the ingestion is reduced by a certain percentage REDUC. The organic matter contents of the soil, then the total energetic value of the soil ingested by the worm and, at last, the variations of its weight are calculated. The new weight (W) of the worm is registered among its attributes.

If the weight variation has been negative, the counter of successive days with negative growth (DP.NEG) is increased by 1 if the worm is active, 0.5 if it is quiescent.

If the weight has increased, the DP. NEG counter is adjusted to zero; if the worm belongs to the reproductive set (W > WREP, a predetermined value) the counter of consecutive days with positive growth (DP. POS) is increased by 1.

f. Mortality submodel

In the Lamto savannas, earthworm mortality essentially occurs during dry periods. At this time, soil ingestion decreases and the earthworms go deeper into the soil in search of more favourable moisture conditions. Thus they ingest a poorer soil and die after having weight loss. Most often, they become quiescent : rolled up in small chambers whose walls are covered by their own fine grained excrements, the worms will resist longer. Another cause of mortality may be senescence, particularly in individuals older than two years.

An empirical system has been established from the above observations in order to calculate mortality rates. When the variation of weight is negative during five consecutive days for the young (weighing from 0.1 to 1 g), 15 days for the immatures (1 to 2 g) and 25 days for the adults (more than 2 g), mortality occurs with the daily probability PROP. DECES.

If W is less than 0.02 g or if the age exceeds the limit of age AGELIM, death occurs automatically.

g. Migration submodel

Populations of *M. anomala* are generally concentrated in the upper ten centimeters of the soil and individual growth is greater between 2 and 10 cm. In the other strata, the young grow slower and the adults lose weight (LAVELLE, SOW & SCHAEFER, 1980).

Worms may however leave these strata when moisture or temperature conditions force them to do so : they will move along the gradients towards a stratum where their existence is not endangered by heat, drought or inundation. Such movements are perceptible all along the year and affect differently the adults and the youngs (LAVELLE, 1971, 1982).

In the model, the migration of each active worm is given by the algebric mean of two independent potential movements along the moisture and temperature gradients. If HUM is less than 12 % the potential movement DH1 is given by the formula : $DH1 = \frac{HUM.W - HMOY}{H1CM}$ where HMOY is the moisture preferendum and H1CM a speed parameter.

If HUM.W is greater than 20 %, the worms move towards a drier stratum in the same way.

If temperature, TEMP.W, is less than 27° C the worms move DH2 cm towards a hotter area; DH2 is equal to :
$\frac{TEMP.W - TMOY}{T1CM}$ where TMOY is the thermic preferendum and T1CM a speed parameter. If TEMP.W is greater than 29° C, the worm will move towards a fresher area.

b. Reproduction submodel

Adults can reproduce when they weigh between 2.6 and 3.0 g, the exact weight depending on population biomass. Cocoon laying generally occurs after a certain number (DP.POS) of successive days with positive growth. However, if the soil is flooded (HUMW < INOND, a limit value), cocoon laying is delayed until the latter dries sufficiently.

The production of cocoons varies between 1 and 3 according to population biomass and their weight is proportional to that of the adults. After each set of cocoons is laid, the adult suffers a decrease in weight equal to the weight of the cocoons and a physiological stress (STR. PONTE) that increases the mortality risk.

If worm weight becomes less than the limit WREP, the worm is taken off the reproductive set. After cocoon laying, DP.POS is put at zero.

3. Incubation process

After cocoons have been laid, an incubation period begins. It will last 23 favourable days *i.e.* with a soil moisture greater than the predetermined incubation threshold. Unfavourable days are not counted. Incubation ends with hatching.

4. Hatching event

When a cocoon achieves the incubation period, a worm aged 0 is born, at the depth where the cocoon was laid, active, and whose DP.NEG is a function of STR. NAISS, a predetermined percentage of the threshold DP.NEG, that takes into account the physiological stress due to hatching.

III. Results of the simulation

The model thus designed has some fixed elements, the set of empirical relationships established from field and laboratory experiments and observations, whose value has been determined by successive approaches when calibrating the model.

The following values have been given to those parameters : REDUC, 10 %; WREP, 2.8 g; DP.POS, 15 days; PRO.DECES, 5 %; AGELIM, 780 days; H1CM, 12.5; HMOY, 16 %; T1CM, 12.5; TMOY, 28° C; INOND, 17 %; STR. NAISS, 50 %; STR. PONTE 50 %.

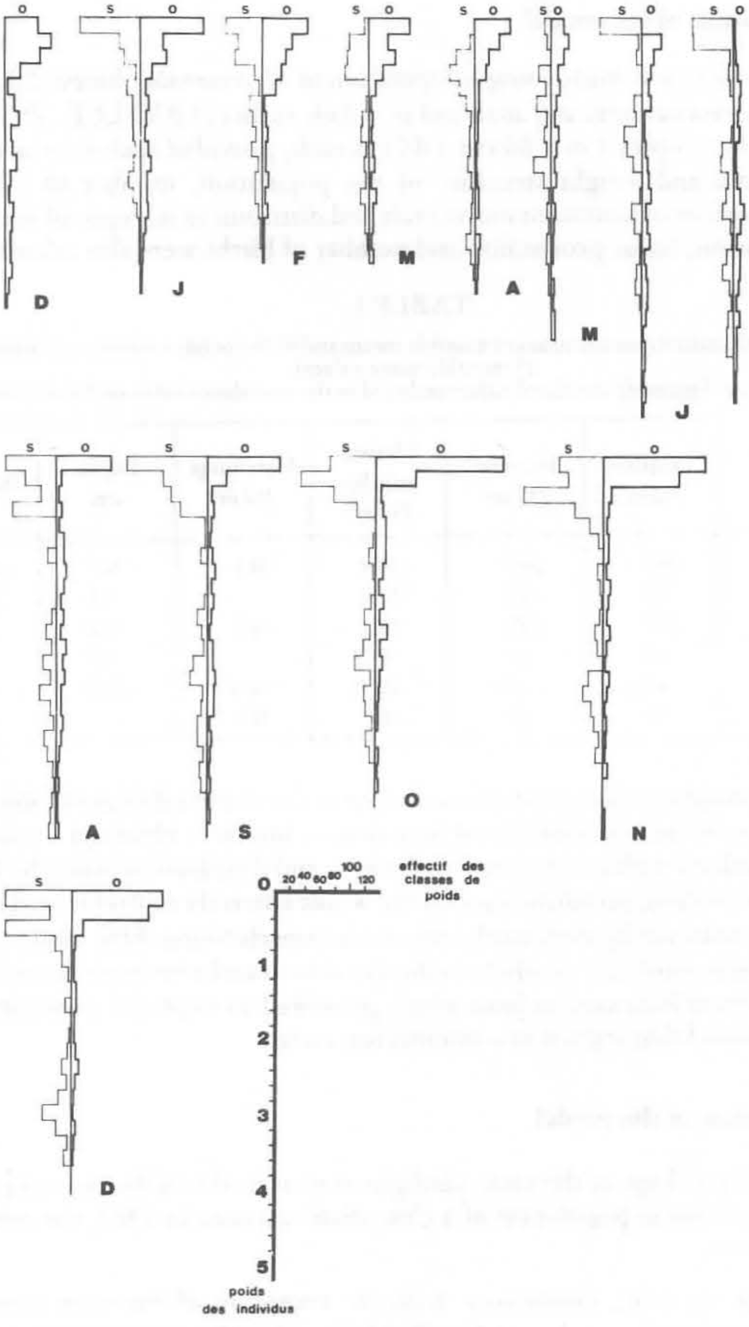

Figure 3 Monthly variations of the weight structure of simulated (S) and observed (O) populations in the calibration of the model.

1. Calibration of the model

The calibration was made using a population of *M. anomala* observed during the year 1972 in a grass savanna and analyzed in details earlier (LAVELLE, 1977, 1978). Twelve monthly samples 1 m x 60 cm x 40 cm each, provided such data as monthly density, biomass and weight structure of the population, number of incubating cocoons, proportion of quiescent individuals and distribution in depth of the population. Soil ingestion, tissue production and number of births were also calculated.

TABLE I

Global results of calibration (annual means of monthly means and 95 % confidence limits calculated with the 12 monthly mean values).
VS % = proportion of monthly simulated values included in the confidence limits of the observed values.

	Density /12 m^2	Biomass /12 m^2	Mature adults /12 m^2	Hatchings /12 m^2	Depth cm	Soil ingestion t/ha
Simulated	240	287	32.4	443	6.7	672
2 SE	55	70	17.0		1.5	
Observed	254	295	32.1	420	8.8	822
2 SE	48	47	9.7		1.2	
Difference %	+5.5	-2.8	+0.9	+5.5	-23.0	-18.2
VS %	75	58	50	50		

The mean results of the simulation are close to the observed values (Table I). The greatest differences are observed in soil ingestion — but the « observed » value is the result of calculations with a certain risk of error — and distribution in depth. The seasonal variations of these parameters are on the whole correctly reproduced. The differences may be explained by some easily detectable imperfections of the model (Fig. 3) : a slightly excessive mortality of adults in the dry season and a too rapid growth of the young worms from February to June which provoked an excessive precocity of the reproductive period that started two months too early.

2. Validation of the model

The model was kept in the same configuration as in the calibration and used to simulate the earthworm population of a clear shrub savanna in 1969, the driest year observed at Lamto.

The results are quite satisfactory with the exception of the mean number of mature worms underestimated in 44.4 % (Table II). The other parameters are approached in about 15 %, and the monthly variations are quite well simulated, especially in the second half of the year (Fig. 4).

TABLE II

Global results of calibration (see Table I).

	Density /12 m^2	**Biomass /12 m^2**	**Mature adults /12 m^2**	**Hatchings /12 m^2**	**Depth cm**	**Soil ingestion t/ha**
Simulated	92	74	3.0	163	11.3	232
2 SE	16	15	2.0		2.1	
Observed	106	86	5.4	140	14.2	Not calculated
2 SE	28	23	2.6		1.9	
Difference %	-13.2	-14.0	-44,4	+16,4	+13,4	
VS %	83	75	60	50	42	

The imperfections already noted in the calibration exert the same effects, an excessive mortality in the dry period, a too rapid growth of the young at the beginning of the rainy season and a too deep localization of the population in the soil.

However, it is encouraging that the validation gives quite good results in spite of conditions very different from those of the calibration : the soil was different, the savanna was a clear shrub one and the year 1969 was a very dry one, which led to a prolongated inactivation of the individuals, a deeper distribution and an important reduction of density, biomass and natality. All these phenomena were correctly reproduced by the model.

IV. Discussion

ALLEZ-LES-VERS has permitted satisfactory simulation of the functioning of a population of *M. anomala* observed in 1972 in a grass savanna and utilized for its calibration. That year, the soil moisture was most often favourable to the activity of earthworms, excepting some dry periods of short duration and one month of flooding. The worms were distributed rather close to the soil surface (7.2 cm on average). A high density (21.2/m^2) kept the intraspecific competition to a high level; this reduced the individual growth and adult fecundity and resulted in a relatively reduced Production to Biomass ratio (2.2). 386 cocoons were produced on the sampling area of 12 m^2, by a mean number of 32.4 adults, that is to say 11.8 cocoons/adult.

Validation was made using the data obtained with the population observed in 1969 in a clear savanna with different soil and vegetation. The year was the driest observed till that date at Lamto which reduced in 8.8/m^2 the mean annual density, *i.e.* 2.4 times less than in the precedent example. Earthworm activity was interrupted for 22 weeks because of drought conditions. The maintenance of the population was

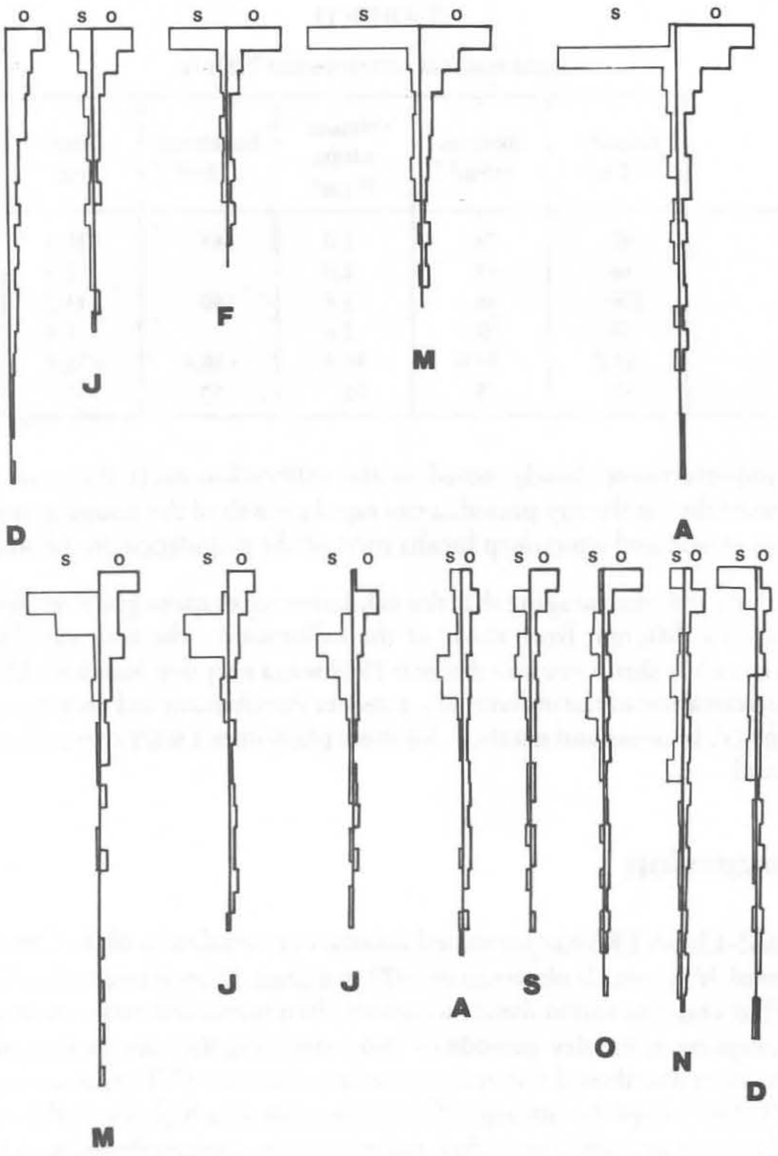

Figure 4 Monthly variations of the weight structure of simulated (S) and observed (O) populations in the validation of the model (see Fig. 3).

clearly due to the protecting effect of quiescence which reduced mortality during this critical period, to a rapid growth of the young worms when they happened to be active and to an increase in the fecundity of surviving adults (101 cocoons produced by a mean number of 3 mature adults, *i.e.* 33.7 per adult which is 3 times greater than in the other simulated population). The resulting P/B ratio was rather high (2.6).

These effects were simulated satisfactorily and the model thus allows the simulation of the different « strategies » used by the populations : individual protection and the use of mechanisms that ensure the rapid return to an optimal activity level, when conditions are favourable, or limitation of this activity when persistant favourable conditions lead the population to the limit of the biotic capacity of the environment. The model also reproduces the rapid modifications of populations which allow them to adapt to seasonal changes in the environment : a reduction of density and biomass in the dry season and the attainment of maximum activity in the last month of the year, when litter is abundant and temperature and moisture are best for earthworm activity.

ALLEZ-LES-VERS will be improved in order to eliminate the defects observed at this stage of its elaboration. Seasonal variations of the soil nutritive value will be taken into account. It should be less at the beginning of the rainy season when the bush fire has destroyed all the litter, than at the end of it, when rains percolating through the restored litter enrich the soil in highly energetic water soluble substrates. The migration model will be improved too, adding the effect of the vertical gradient of organic matter which will result in a movement of earthworms towards the stratum -2 to -10 cm which they prefer, in the absence of any other stimulation. When these defects will be corrected, a certain indetermination will remain due to the difficulty of fixing the attributes of earthworms at the beginning of the simulation, to the imperfections of the environment submodel and also to the relative uncertainty of some observed data.

Simulations performed with other observed populations will show whether ALLEZ-LES-VERS is able to simulate their functioning whatever the environment conditions may be. At a further stage, the use of the model will be extended to other species. Its logic and structure will be kept, but the diverse empirical relationships and parameters will have to be adapted. Studies are being carried out with this purpose on populations of the mesohumic endogeous *Pontboscolex corethrurus* in Mexican tropical ecosystems (LAVELLE & CRUZ, 1983). In this case, ALLEZ-LES-VERS will be used for the ecological monitoring of a nuclear power plant.

The model should then be generalized to all the earthworm species : some structural transformations will be made to take into account the physiological characteristics of some of them (e.g. the diapause of true anecics) and factors that were unimportant for *M. anomala* and *P. corethrurus* such as cold or predation.

This model will make it possible to control the populations subjected to particular effects and foreseeing their evolution. It will be very useful in the adaptation of alternative agricultural practices which would take into account and try to improve the activity of these inexhaustible workers of the soil.

Acknowledgements

We are greatly indebted to Drs. A. CARTER and S. VINOGRADOV for the revision of the text.

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Discussion

HASSALL, M. : How would the inclusion in the model of mortality factors acting in the field, such as predation, which do not involve the animals losing weight affect the simulation ?

LAVELLE, P. : Predator populations are quite scarce within the soil of Lamto savannas. As far as other factors are concerned, their effect will be really important when the worms are in a weak physiological state; then, infections, parasitism or senescence will have stronger effects, we take them into account in the mortality submodel.

KRETZSCHMAR, A. : La comparaison des courbes simulées et observées fait souvent apparaître une inertie du modèle par rapport aux données. Cela est-il dû aux caractéristiques intrinsèques des fonctions choisies pour les différents modèles ou bien aux valeurs des coefficients dont les fonctions sont affectées ?

LAVELLE, P. : L'inertie observée provient d'un défaut du modèle : la mortalité excessive des adultes en saison sèche (l'effet protecteur de la quiescence est encore sous-estimé dans cette simulation). Cette mortalité accrue entraîne une diminution anormale de la densité. La reproduction est d'abord réduite puis augmente à mesure que d'autres vers deviennent adultes; ce n'est que quelques mois plus tard que les valeurs simulées rejoignent les valeurs observées.

VAN STRAALEN, N.M. : Were your laboratory results, on which the structure of the model and its different coefficients are based, inadequate in order to explain that some calibration of the model using field data was necessary ?

LAVELLE, P. : The model is built *both* with results of laboratory cultures (in the case of parameters that cannot be measured in the field) and field observations. The aim of the simulation is to reproduce changes occurring in a natural population; therefore first, it is necessary to *calibrate* (= adjust the parameters) the model to a first population, then, to *validate* it using the same parameters in the simulation of another population.

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